

## Diffuse Knapweed (*Centaurea diffusa*) Seed Germination

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The objective of this study was to define further the environmental requirements for safe sites for germination of diffuse knapweed achenes (seeds). Germination temperature profiles were developed for diffuse knapweed seeds collected from sites in the Great Basin and Colorado. Each profile consisted of seeds germinated at 55 constant or alternating temperatures from 0 through 40 C. The resulting germination was used to develop quadratic response surfaces with regression analysis. Some germination occurred from 71 to 96% of the temperature regimes, depending on the accession being tested. Maximum observed germination ranged from 85 to 98%. Optimum germination, defined as the maximum observed minus one half the confidence interval at the 0.01 level of probability, occurred at a wide range of temperatures from cold periods of 0 through 20 C, alternating with warm periods of 10 through 35 C. The temperature regimes that most frequently supported optimum germination were 5/25 C (5 C for 16 h and 25 C for 8 h in each 24-h period) and 10/25 C. Germination of diffuse knapweed seeds was generally higher at alternating than constant temperatures.

**Nomenclature:** Diffuse knapweed, *Centaurea diffusa* Lam. CENDI.

**Key words:** Invasive weeds, seedbed ecology, range weeds.

Diffuse knapweed is a member of the *Centaurea* genus, which includes approximately 500 ill-defined species in the Asteraceae family. The *Centaurea* genus includes some of the most serious exotic, invasive weed species on rangelands in western North America. Diffuse knapweed is a native species of southeastern Europe that was introduced to North America in approximately 1900, and by the mid 1990s it occupied 1.2 million hectares in the western United States (Lacey 1989; Roché and Roché 1988); furthermore, diffuse knapweed spread from 9 to 28 counties in the Pacific Northwest between 1950 and 1975 (Roché and Talbot 1986). Diffuse knapweed invasion has reduced biodiversity, forage for livestock and wildlife, and deteriorated watershed characteristics (Lacey et al. 1989). This exotic species is highly invasive in rangeland plant communities, ranging from heavily grazed areas to those in high ecological condition (Lacy et al. 1990).

In the Pacific Northwest of North America, diffuse knapweed is a biennial (i.e., Sheley et al. 1997); however, unique incidences of annual short-lived perennial growth forms have been reported (Keil and Turner 1993; Thompson and Stout 1991). In Europe the growth habit is considered to be annual or biennial, but not perennial. The species is best described as a semelparous perennial where flowering is dependent on plant size and vernalization (Thompson and Stout 1991). Diffuse knapweed seedling establishment can occur in the spring or fall. After establishment the plant grows in a rosette form until a critical developmental stage is reached and it then bolts and flowers (Thompson and Stout 1991). These multibranched plants are 2 to 8 dm tall with varying amounts of a gray tomentose. The flower color is highly variable and includes pink (most common), white, and pale purple (Keil and Turner 1993). This is one of the few *Centaurea* species that is an invasive weed in North America with achenes (seeds) that have no pappus or occasionally have very short white teeth. The seeds of most *Centaurea* growing in North America have abundant pappus or bristles on the seeds.

Although diffuse knapweed is a native species of southeastern Europe, it has a natural range that extends to north

central Ukraine (Tutin et al. 1976). It is difficult to determine the native range of diffuse knapweed because the species now occurs as an invasive weed in much of central Europe. Diffuse knapweed has been observed growing at elevations from 150 to 900 m in Canada (Watson and Renny 1974) and at elevations up to 2,600 m in the United States (Sheley et al. 1998). The distribution of diffuse knapweed in the western United States is most continuous in the Pacific Northwest, but extends over much of northern California and as far south as central Arizona (Sheley et al. 1998). In the western Great Basin, diffuse knapweed infestations are largely ruderal, geographically disjunct, and highly persistent despite weed control efforts.

Diffuse knapweed seed germinate under a wide range of environmental conditions (Sheley et al. 1998). Germination was reported to occur at temperatures ranging from 7 to 34 C with optimum germination at 24 C (Watson and Renny 1974). Nolan and Upadhyaya (1988) present a very different picture of diffuse knapweed germination in that they suggest that large numbers of seeds are dormant when incubated at 25 C. This dormancy could be overcome with addition of gibberellic acid, exposure to red light, or excision of the distal end of the seed.

The invasive species of *Centaurea* introduced to North America have a potential for annually producing huge seed crops. Only a tiny amount of this annual seed rain is necessary to perpetuate the diffuse knapweed stands (Schirman 1981; Sheley et al. 1997). Schirman (1981) suggested this amount was 0.1% of the annual seed rain. He also reported the extreme variability in seed production per plant among years in apparent relation to moisture available for plant growth. The grossly excess annual seed rain may have great significance in the building of seed banks for *Centaurea* species (Callihan et al. 1993), but raises the question of the specific inherent potential of the seeds that do germinate and establish in relation to safe sites for germination in seedbeds (Harper 1977).

Our purpose in this study was to quantify the occurrence and magnitude of diffuse knapweed seed germination in relation to a broad spectrum of potential seedbed temperatures. This information provides one parameter for the understanding of safe sites for germination of seeds of this species.

DOI: 10.1614/WS-D-10-00007.1

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Table 1. Germination parameters calculated from quadratic response surfaces (Young and Evans 1982).

Parameters	Derived parameter	Purpose
Calculated within profile		
Mean germination	Sum divided by 55	Gross comparison of profiles
Percentage of regimes with germination	Number with germination divided by 55	Indication of breadth of germination response
Percentage of regimes with optimum germination	Number of regimes with germination not less than maximum observed minus $\frac{1}{2}$ confidence interval divided by 55	Provides indication of the breadth of temperatures that support optimum germination
Mean of optima	Sum of optima divided by number of optima regimes	Provides measure of potential germination at adapted temperatures
Maximum germination	Highest observed germination	Indication of potential viability
Calculated among germination profiles		
Frequency of optima	Times temperature regimes supports optima divided by total number of profiles	Provides an estimate of optimum temperatures for germination with precision

## Methods and Materials

At six sites located in Nevada and Colorado diffuse knapweed seeds were collected from as many different plants as possible, over the distribution of the individual infestations. Seeds were collected at maturity which ranged from late July to early September depending on the year and elevation of the site. The seed heads at each site were combined and allowed to reach moisture equilibrium, and then threshed. The cleaned seeds were randomly sampled to provide the 5,500 seeds necessary for each germination-temperature experiment. Collection sites and years of collection include: Bordertown, Nevada, 2002 through 2003 (39°38', 119°58'); Reno, Nevada, 2004 (Arrow Creek 39°24', 119°45', and Thomas Creek 39°25', 119°47'), and Colorado (location not specified). The seeds were stored in paper bags at laboratory temperature (22 C) for 3 mo after harvest.

In all experiments, four replications of 25 seeds each were used in a randomized block design (temperature regimes). Seeds were placed on top of nontoxic commercial germination paper<sup>1</sup> in closed plastic Petri dishes (100 × 100 × 15 mm) and kept wet with tap water. Germination trials were conducted in dark germinators and physically transferred to each incubation temperature. Seeds were considered germinated when the radicle emerged at 5 mm. Germination counts were made after 1, 2, and 4 wk and total germination was recorded. Constant incubation temperatures were 0, 2, and 5 C and at 5° increments through 40 C ( $\pm 0.2$  C). Alternating regimes included 16 hr at each constant temperature, plus 8 hr at each possible higher temperature per 24 hr. For example, 35 C alternated with 40 C only, whereas 0 C alternated with 2, 5, 10, 15, 20, 25, 30, 35, and 40 C. This made a total of 55 constant and alternating temperature regimes in 10 Precision 815 high/low temperature incubators (Young et al. 1973, 1991, 2005).

The germination responses of the accessions of diffuse knapweed were compared with the use of the following categories of seedbed temperature regimes (Young and Evans 1982): (A) very cold: 0/0 (constant 0 C), 0/2 (0 C for 16 hr and 2 C for 8 hr in each 24 hr), 0/5, and 2/2 C; (B) cold: 0/10, 0/15, 2/5, 2/10, 2/15, 5/5, and 5/10 C; (C) cold fluctuating: 0/20 through 0/40 C and 2/20 through 2/40 C; (D) fluctuating: 5/35, 5/40, 10/35, 10/40, and 15/40 C; (E) moderate: 5/15 through 5/40, 10/10 through 10/30 C, 15/15 through 15/35 C, 20/20 through 30/35 C, and 25/25 through 25/30 C; (F) warmer: 20/40, 25/35, 25/40, 30/30 through 30/40, 35/35, 35/40, and 40/40 C. The temperature categories reflect germination environments of field seedbeds

for rangeland weeds based on several years of monitoring (Evans et al. 1970; Evans and Young 1970, 1972).

Data from each base temperature and its alternating temperature regimes were used to generate a quadratic response surface with estimated means and confidence intervals at the 0.01 level of probability (Evans et al. 1982; Palmquist et al. 1987; Young et al. 1980). Several germination parameters were calculated from the quadratic response surfaces (Table 1) (Young and Evans 1982). Among profiles, individual parameters were compared by analysis of variance and the use of Duncan's new multiple range test to separate means.

## Results and Discussion

The extremes in germination-temperature profiles for the seeds of diffuse knapweed we tested are represented in the profiles shown in Tables 2 and 3. The seeds for the profile in Table 2 were collected at the Bordertown site north of Reno, NV from a ruderal stand that has been under attempted eradication by a succession of herbicidal, mechanical, and biological control agent (*Sphenoptera jugoslavica* and *Larinus minutus*) treatments for 20 yr. We have profiles for seeds collected from this stand for three consecutive years (Table 4). We could not collect seed from this stand in 2004 because the level of infestation the biological control agent *L. minutus* virtually eliminated seed production. The profile for 2002 is representative for the population (Table 2). Mean germination for the entire profile is 25%, with 71% of the temperature regimes supporting at least some germination (Table 4). Maximum germination was 98% which occurred at a temperature regime of 2/25 C (2 C for 16 hr and 25 C for 8 hr in each 24-hr period) (Table 2). Optimum germination, defined as not less than the maximum observed minus one half the confidence level, largely occurred at temperature regimes with 25-C warm period temperatures (lone exception 15/20 C): however, a constant 25 C produced only 45% germination (Table 2). Only a constant 10 C produced greater germination than the next colder alternating temperature regime and all 10 C alternating with colder temperatures were below the minimum threshold for germination of diffuse knapweed (Table 2). For all of the profile parameters summarized, there were no significant ( $P \geq 0.01$ ) differences among years of seed production for the Bordertown site.

Apparently, diffuse knapweed seeds are not as well adapted for germination at constant incubation temperatures. The germination research of Nolan and Upadhyaya (1988)

Table 2. Quadric response surface with calculated percentage germination and confidence interval ( $P \geq 0.01$ ) for seeds of diffuse knapweed incubated at 55 constant or alternating temperatures. Seeds collected at Bordertown, Nevada in 2002, test conducted January 2003.<sup>a</sup>

Cold-period temperature (C)	Warm-period temperature (C)									
	0	2	5	10	15	20	25	30	35	40
	Percentage germination (%)									
0	0 + 16	0 + 16	0 + 16	0 + 16	23 ± 14	48 ± 8	58 ± 8	30 ± 9	21 ± 6	0 + 16
2		0 + 16	0 + 16	0 + 16	53 ± 8	83 ± 6	[98 ± 8*]	63 ± 8	23 ± 14	0 + 16
5			0 + 16	0 + 16	53 ± 8	88 ± 6	93 ± 6*	75 ± 9	18 ± 14	0 + 16
10				30 ± 10	85 ± 6	88 ± 6	93 ± 6*	88 ± 6	35 ± 9	21 ± 5
15					68 ± 8	90 ± 7*	93 ± 8*	90 ± 7*	73 ± 9	40 ± 10
20						50 ± 9	70 ± 9	83 ± 8	50 ± 9	38 ± 10
25							45 ± 10	63 ± 9	45 ± 10	21 ± 5
30								21 ± 5	21 ± 5	0 + 16
35									0 + 16	0 + 16
40										0 + 16

<sup>a</sup> Number following the mean is one half the confidence interval as determined from regression equations used to develop the response surface (Palmquist et al. 1987). The maximum calculated germination is enclosed in brackets. The asterisks indicate means not lower than the maximum germination minus one half of its confidence interval, our definition of optimum germination.

reported significant dormancy in diffuse knapweed seeds, but they only used a constant 25-C incubation temperature. Seed dormancy induced by sensitivity to light quality (near red to far red) can be induced to germinate by substantial diurnal fluctuations in temperature, for example, seeds of common mullein (*Verbascum thapsus* L.) (Semenza et al. 1978). Young et al. (2005) reported that even though yellow starthistle (*Centaurea solstitialis* L.) was reported to germinate at higher levels with light (Joley et al. 1997), germination at alternating temperatures reached nearly 100% without light. If such a type of germination restriction exist in diffuse knapweed seeds, the 2/25 C level of diurnal fluctuation in temperature overcomes the dormancy.

Seeds of the Bordertown accession of diffuse knapweed had no germination at very cold seedbed temperature regimes (Table 4). In the intermountain west, where moisture is largely available in rangeland seedbeds during the cold winter and early spring period, failure to germinate at very cold seedbed temperatures would appear to be a serious handicap for at least this accession of diffuse knapweed (Evans et al. 1970; Young et al. 1972). However, the Bordertown stand of diffuse knapweed did spontaneously establish and renew itself for several decades so the seeds are obviously finding a safe site for germination at some period of the year when temperatures are more moderate and moisture is available. The maximum germination observed for this accession occurred at 2/25 C,

which is easily obtainable by midspring at the Bordertown site (Evans et al. 1970). This suggests the lack of germination at very cold constant temperatures and limited diurnal fluctuation temperature regimes is not of great ecological significance to diffuse knapweed; however, other exotic, invasive and potentially competing weeds such as downy brome (*Bromus tectorum* L.) can germinate at these temperatures (Young and Evans 1982).

Germination of diffuse knapweed seeds of the Bordertown accession dropped markedly when the warm period temperatures reached 40 C (Table 2). With 0-C cold period temperature germination dropped markedly when 35-C warm period temperatures were reached. This may suggest that the magnitude of diurnal fluctuations was becoming limiting. A constant 40 C or alternating 30/40 C or 35/40 C also failed to produce germination which suggests that 40 C may exceed the germination potential of diffuse knapweed seeds. Perhaps it is a combination of diurnal fluctuation and duration of excessive temperatures because germination at 15 or 20 C alternating with 40 C was 40 and 38%, respectively.

The accession of diffuse knapweed collected in the southern suburbs of Reno, NV at Arrow Creek and Thomas Creek site produced a germination profile with a greatly enhanced magnitude and breath of germination compared to the Bordertown accessions (Tables 3 and 4). These collections sites are 50 km apart with Arrow Creek/Thomas Creek site

Table 3. Quadric response surface with calculated percentage germination and confidence interval ( $P \geq 0.01$ ) for seeds of diffuse knapweed incubated at 55 constant or alternating temperatures. Seeds collected at Arrow Creek Drive, Reno, NV in 2002, test conducted January 2003.<sup>a</sup>

Cold-period temperature (C)	Warm-period temperature (C)									
	0	2	5	10	15	20	25	30	35	40
	Percentage germination (%)									
0	0 + 12	9 ± 10	27 ± 10	61 ± 8	92 ± 6	95 ± 5*	95 ± 5*	96 ± 5*	54 ± 8	24 ± 10
2		17 ± 10	39 ± 9	76 ± 7	90 ± *	90 ± 5*	90 ± 5*	90 ± 5*	70 ± 7	30 ± 9
5			36 ± 9	77 ± 7	[98 ± 8*]	97 ± 5*	90 ± 5*	88 ± 5	70 ± 7	42 ± 9
10				89 ± 5	97 ± 5*	93 ± 5*	92 ± 6*	90 ± 6*	74 ± 7	46 ± 9
15					92 ± 5*	96 ± 5*	82 ± 6	80 ± 7	60 ± 8	30 ± 9
20						88 ± 6	90 ± 6*	80 ± 7	72 ± 7	22 ± 10
25							80 ± 7	82 ± 7	57 ± 8	15 ± 10
30								64 ± 8	68 ± 8	10 ± 10
35									9 ± 10	2 ± 12
40										0 + 12

<sup>a</sup> Number following the mean is one half the confidence interval as determined from regression equations used to develop the response surface (Palmquist et al. 1987). The maximum calculated germination is enclosed in brackets. The asterisks indicate means not lower than the maximum germination minus one half of its confidence interval, our definition of optimum germination.

Table 4. Summary of germination-temperature profiles for seeds of diffuse knapweed.<sup>a</sup>

	Locations					
	Bordertown, NV			Reno, NV		Colorado
				Arrow	Thomas	
	2001	2002	2003	2004	2004	
Profile and seedbed temperatures	2001	2002	2003	2004	2004	2003
	(%)					
Profile characteristics						
Mean	25 b	26 b	26 b	54 a	50 a	64 a
Regimes with some germination	71 b	71 b	71 b	96 a	94 a	96 a
Mean of optima	85	94	94	94	93	95
Regimes with optima	2 b	7b	5 b	31 a	16 b	46 a
Maximum	85 b	98 a	98 a	98 a	96 a	100 a
Regime with maximum	2/25 C	2/25 C	2/25 C	5/15 C	5/25 C	Multiple
Seedbed temperatures						
Very cold	0	0	0	13	4	3
Cold	39 b	40 b	18 c	76 a	78 a	87 a
Cold fluctuating	36 b	40 b	40 b	73 a	66 a	77 a
Fluctuating	13 c	18 c	18 c	52 b	51 b	87 a
Warmer	8 b	10 b	10 b	23 b	27 a	37 a
Moderate	53 d	68 bcd	68 cd	84 ab	74 bc	94 a

<sup>a</sup> Means within rows followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's new multiple range test. No letter indicates no significant differences.

being 150 m lower in elevation. The collection site is now located in an urban area that has sprawled over former irrigated meadows and big sagebrush (*Artemisia tridentata* L.)/bunchgrass rangeland. Diffuse knapweed infestations existed in the area before urbanization and were subject to herbicidal and biological weed control efforts. *Larinus minutus*, which decimated diffuse knapweed seed production at Bordertown (where it was not deliberately released to the best of our knowledge) was released at the Arrow Creek site, but apparently did not establish (communication from Jeff Knight, State Entomologist, Nevada Department of Agriculture).

Mean germination for the Arrow and Thomas Creek accessions was 54 and 50%, roughly double the mean for the Bordertown accession (Table 3 and 4). The breadth of the germination response also expanded with only the constant 0- and 40-C regimes having no germination for the Arrow Creek accession and 0/2 C also having no germination for the Thomas Creek accession. Germination at a constant 25 C increased from 45% for Bordertown to 80% for the Arrow Creek accession and 62% for the Thomas Creek accession (Tables 2 and 3). This is the temperature where Nolan and Upadhyaya (1988) found multiple types of dormancy for diffuse knapweed seeds. As was the case with the Bordertown accession, germination at 25-C warm periods increased with diurnal fluctuation (Table 3). The temperature regimes that supported optimum germination increased from 2 to 7% for the Bordertown accessions to 31% for the Arrow Creek accession. The Thomas Creek accession was not significantly higher ( $P \geq 0.01$ ) than the Bordertown accession (Table 4). The maximum observed germination (98%) for the Arrow Creek accession occurred at 10/15 C, a temperature where the Bordertown accessions had only about 50% germination.

The single accession from Colorado had the highest germination in all germination temperature profile parameters that were compared. As with all other accessions tested the Colorado seed had low germination at very cold temperature regimes with a huge increase in germination at cold temperature regimes (Table 4).

Without planting the different accessions in a common garden and testing the seed produced, it is impossible to determine if the variation among accessions is inherent or a product of different maternal environments. If you plot the frequency that a given temperature regime supported optimum germination for all accessions of diffuse knapweed tested (Table 5), there are 28 temperature regimes that supported optimum germination at least once. These range from a low of 2/10 C to a high of 20/35 C. The temperature regime that most frequently supported optimum germination was 5/25 C and 10/25 C. The only constant temperatures that supported optimum germination were 15 C (33%) and 20 C (17%) (Table 5).

What is the ecological significance of limited germination at very low, high, or widely fluctuating temperature regimes? It has long been recognized that three basic germination strategies exist in seeds of invasive weeds (Newman 1963; Salisbury 1942; Young et al. 1968): (1) simultaneous, (2) continuous, and (3) a combination of both simultaneous and continuous germination. The rationale in simultaneous germination is the first species to germinate and preempt environmental potential in the seedbed has an advantage in subsequent competitive relations or potentially in interference for actual safe sites for germination. The risk with this strategy is the entire seedling population can be lost to drought, weed control, or predation without a seed bank to give the species a second chance. Continuous germination avoids the pitfalls of a portion of postemergence disasters at the ecological deficit of, by definition, not completely winning the race for preemption of environmental potential in seedbeds. Obviously, being able to combine both strategies would be the best of both worlds. One method of accomplishing the combination approach is to produce seeds with the inherent potential for simultaneous germination if they find sufficient safe sites in seedbeds. Those that fail to find safe sites acquire a dormancy that breaks down in response to time and environmental stimuli, producing a de facto state of continuous germination. This is the germination system found in the exotic, invasive downy brome (Young et al.



Table 5. Frequency that a given temperature regime supported optimum germination for seeds of diffuse knapweed.

Cold-period temperature (C)	Warm-period temperature (C)									
	0	2	5	10	15	20	25	30	35	40
	Percentage germination (%)									
0					33	33	33	17		
2			17	33	33	50	17			
5				50	66	83	33	17		
10				50	66	83	33	17		
15				33	50	66	17	17		
20					17	50	17	17		

1968). A second way to accomplish the combination of simultaneous and continuous germination is for the plant to produce seeds with phenotypically variable germination requirements. This system is well represented by the native perennial Indian ricegrass (*Achnatherum hymenoides* Roemer & Schultes) (Blank and Young 1992). Sheley and Larson (1996) suggest that continuous seedling emergence may allow diffuse knapweed to occupy all available safe sites for germination. Perhaps, diffuse knapweed accomplishes continuous germination by producing seeds with a wide variation in amplitude of temperature tolerance for germination. Give them the right temperature and they virtually all germinate, but a few can germinate at such extremes as 0/2, 35/40, or even 0/40 C.

## Sources of Materials

<sup>1</sup> Steel blue blotter paper, Anchor Paper, St. Paul, MN.

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Received January 18, 2010, and approved April 14, 2010.